TAXONOMY OF *STENARIA* (RUBIACEAE: HEDYOTIDEAE), A NEW GENUS INCLUDING *HEDYOTIS NIGRICANS*

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ABSTRACT

Five North American species formerly in the genus *Hedyotis* (Hedyotideae; Rubiaceae) are revised and placed in the newly recognized genus *Stenaria*, a name used by Rafinesque for a subgenus in the genus *Houstonia*. Keys, descriptions, distributions, and synonymies are provided. The principal species is *Stenaria nigricans*, a wide-ranging polymorphic species native to eastern, central, and southwestern United States and northern and central Mexico. The remaining species are *S. butterwickiae*, known only from Brewster Co., Texas; *S. mullerae* of Coahuila, Mexico, and Brewster Co., Texas; *S. rupicola* of southwestern Texas and northern Coahuila, Mexico; and *S. umbratilis*, rare and disjunct in northern Mexico south to Veracruz. Varieties are recognized within *S. mullerae*, *S. nigricans*, and *S. umbratilis*.

RESUMEN

Se revisan cinco especies de Norte América anteriormente incluidas en el género *Hedyotis* (Hedyotideae; Rubiaceae) y se incluyen en el género nuevo y reconocido *Stenaria*, un nombre usado por Rafinesque para un subgénero dentro del género *Houstonia*. Se presentan claves, descripciones, distribución, y sinónimos. La especie principal es *Stenaria nigricans*, una especie polimorfa de amplia distribución, y nativa de las zonas orientales, centrales, y sudoeste de los Estados Unidos así como de la parte norte y central de México. Las otras especies son *S. butterwickiae*, conocida únicamente de Brewster Co., Texas; *S. mullerae* de Coahuila, México y de Brewster Co., Texas; *S. rupicola* del sudoeste de Texas y norte de Coahuila, México; y *S. umbratilis*, especie rara y disyunta de la parte norte de México al sur de Veracruz. Se reconocen variedades de *S. mullerae*, *S. nigricans*, y *S. umbratilis*.

Stenaria, newly recognized at generic rank, includes the widely distributed polymorphic species, *Hedyotis nigricans*, and four other related species that occur in the southwestern United States or Mexico: *Hedyotis butterwickiae*, *H. mullerae*, *H. rupicola*, and *H. umbratilis*. This group of five species has been called the *Hedyotis nigricans* group (Terrell 1996a).

The choice of a type species for the genus *Hedyotis* has been the subject of some controversy regarding which of two Linnaean species, *H. auricularia* or *H. fruticosa*, should be selected. *Hedyotis auricularia* has oldenlandioid seeds, although they differ slightly from typical species of *Oldenlandia*. Seeds of *H. fruticosa* are quite different from those of *H. auricularia*. Conservation of the name *H. fruticosa* as type would avoid disruption in *Oldenlandia* nomenclature.

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Whichever name is chosen, the genus name *Hedyotis* does not apply to the *Hedyotis nigricans* group, which has seeds differing entirely from the seeds of either *H. auricularia* or *H. fruticosa*; consequently a new name is needed for the *H. nigricans* group. Rafinesque's name for a subgenus of *Houstonia*, subg. *Stenaria*, is here elevated in rank as the name for the new genus.

Seed characters are very important in the classification of the tribe Hedyotideae (Terrell et al. 1986; Terrell 1991, 1996a). The species of *Houstonia* were grouped into subgenera and sections based mainly on seed morphology and chromosome number (Terrell 1996a). Certain *Houstonia* species (e.g., *H. rubra* Cav. and *H. subviscosa* (Wright ex A. Gray) A. Gray) differ considerably in corolla size and somewhat in corolla morphology, but nonetheless have similar seed morphology and the same chromosome number, and are classified in the same section. Thus, corolla morphology by itself may be misleading as a taxonomic character. It is likely that research on other tribes of the Rubiaceae will demonstrate the importance of seed morphology; for example, *Diodia* and *Richardia* in the Spermacoceae differ greatly in seed morphology from the Hedyotideae. Robbrecht (1989) successfully utilized pyrene and seed characters in studying *Chazaliella* in the African Psychotrieae.

Hedyotis nigricans differs from *Houstonia* in having a chromosome number of x=9 or 10 (chromosome data in this group are known only for *H. nigricans*) and non-crateriform seeds, which are somewhat compressed and ellipsoid with a centric punctiform hilum (Fig. 1). In contrast, the 20 species of *Houstonia* have basic chromosome numbers of 6, 7, 8, and 11, and crateriform seeds (with a ventral depression occupied by a linear hilar ridge or having a ventral subglobose cavity without a hilar ridge); these were discussed and illustrated by Terrell (1996a). The genus *Oldenlandia* has a chromosome number of x=9, but differs entirely in having very small, numerous, 3-angled seeds. *Hedyotis nigricans* has been seen growing naturally in the same habitat or near species of *Houstonia* and *Oldenlandia* without any evidence of hybridization, nor have any hybrids been found in herbaria. *Hedyotis nigricans* var. *nigricans* is widely distributed in the United States and Mexico, and differs conspicuously from *Houstonia* and *Oldenlandia* species by having elongate capsules instead of globose ones, as well as by having seeds differing as already described.

A related group is the presently recognized *Hedyotis mucronata* group, mostly native to Baja California. These eight species have a chromosome number of x=13 and ellipsoid or dorsally strongly ridged seeds with punctiform hila.

SYSTEMATIC TREATMENT

Stenaria (Raf.) Terrell, stat. nov. TYPE SPECIES: *Stenaria nigricans* (Lam.) Terrell.
Houstonia subg. *Stenaria* Raf., Ann. Gen. Sci. Phys. 5:226. 1820. LECTOTYPE, here designated: *Houstonia rupestris* Raf., Ann. Gen. Sci. Phys. 5:226. 1820 [=*Hedyotis nigricans* (Lam.) Fosb.]

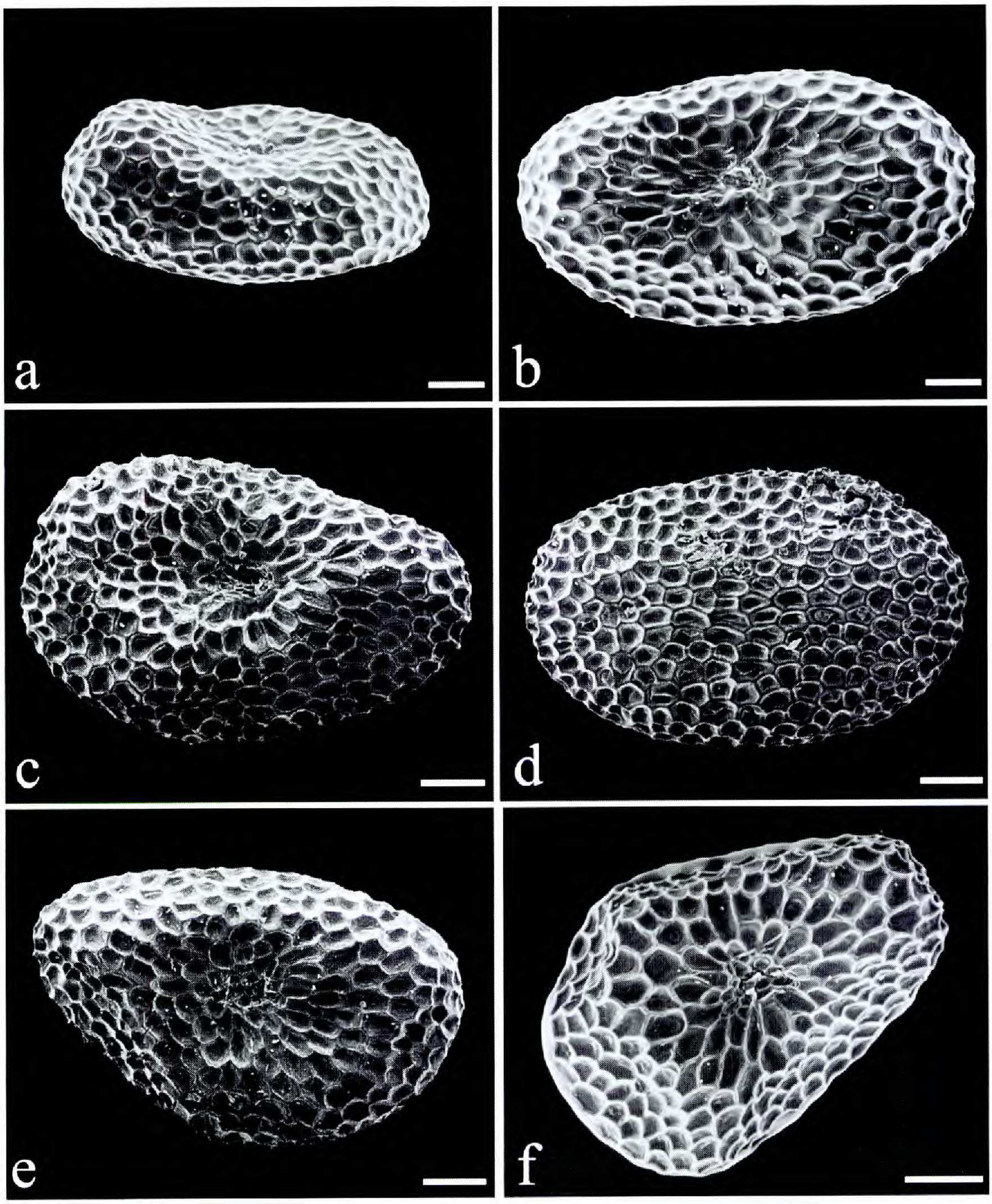

FIG. 1. Seeds of *Stenaria* species. a. *S. nigricans*, ventral view showing centric hilum, tilted 50°. b. *S. nigricans*, ventral view, not tilted. c, d. *S. mullerae*, ventral and dorsal views. e. *S. rupicola*, ventral view. f. *S. umbratilis*, ventral view. Bars=0.1 mm. *S. nigricans, Terrell 3923* (US), Manitee Co., FL; *S. mullerae, Chiang et al. 9421* (TEX), Coahuila; *S. rupicola, Tharp 43-866* (TEX), Pecos Co., TX; *S. umbratilis, Johnston et al. 12032B* (TEX), Coahuila.

Houstonia [unranked] *Angustifoliae* Small, Man. S.E. Fl. 1254. 1933. TYPE: *Houstonia angustifolia* Michx. [=*Hedyotis nigricans* (Lam.) Fosb.]

Rafinesque included his new species *Houstonia rupestris* as the first species in his new subgenus *Stenaria*. He also included four other species now in

Houstonia. Three (*H. heterophylla* Raf., *H. oblongifolia* Raf., and *H. obtusifolia* Raf.) of these are nomina dubia, and the fourth is *H. tenuifolia* Nutt. (=*H. longifolia* Gaertn. in Terrell 1996a). Steudel (Nom. Bot. ed 2, 1:776. 1840) listed *Stenaria* (as a nomen nudum) in smaller letters under *Houstonia*, consequently, he apparently intended *Stenaria* as a taxon ranked below *Houstonia* or else as a synonym of *Houstonia*.

Perennial herbs or low shrubs with or without woody tap root. Stems 2–62 cm tall, often from woody base, stout to slender, erect, spreading, or prostrate, glabrous to pubescent. Leaves 2–40 mm long, 0.3–8 mm wide, sessile or on short petioles, filiform or linear to ovate-lanceolate, elliptic, or oblanceolate, glabrous to pubescent. Stipules 0.5–3.5 mm long and wide, scarious, ovate, deltate, or lanceolate, sometimes acuminate or caudate, 0–few toothed or entire. Inflorescence of few-many cymes, dense to diffuse, flowers heterostylous or apparently homostylous in *S. umbratilis*, sessile or pedicellate. Hypanthium (calyx cup) hemispherical or cup-shaped, glabrous to hirsute. Calyx lobes 0.5–3 mm long, 0.2–1 mm wide, narrowly lanceolate to ovate-lanceolate, margins glabrous to ciliate, apices obtuse, acute, or mucronate. Corollas 2–8.5 mm long, salverform or funnelform, white, purple, pinkish, or lavender; tube 1.5–5.5 mm long, 0.4–1 mm wide at base, 0.5–2.5 mm wide at throat, densely puberulent or pubescent within; lobes 4(–5), 1–4.5 mm long, 0.5–2 mm wide, lanceolate or ovate, densely pubescent or puberulent on inner faces, apices glabrous or hairy. Pin form with stigmas subglobose, broadly elliptic,or oblong, their lobes 0.2–1.3 mm long, pubescent, elliptic or linear, exserted 0.5 to 3.5 mm beyond corolla throat; anthers 4(–5), 0.8–1.8 mm long, linear or narrowly oblong, inserted at midpoint or at distal end of corolla tube or with tips exserted at corolla throat. Thrum form with anthers 0.6–2 mm long, narrowly oblong or linear, usually blue or white, straight or curved, on slender or flattened filaments ca. 0.5–2.5 mm long, located at mouth of corolla tube or somewhat exserted; stigmas ca. 0.3–0.8 mm long, included, extended to near midpoint or to distal end of corolla tube. Mature capsules 1–4.5 mm long, 1–2.7 mm wide, 1/2–3/4(–4/5) inferior, dehiscing loculicidally, somewhat compressed, turbinate, obovoid, ellipsoid, or subglobose, glabrous to hirsutulous. Seeds several to 26 or more per capsule, 0.4–1.15 mm long, 0.3–0.6 mm wide, black or brown, often shiny, slightly to somewhat dorsilaterally compressed, non-crateriform, ellipsoid, in outline elliptical, oblong, or slipper-shaped, ventral face with punctiform centric hilum on flat, slightly convex, or slightly ridged surface, testa finely reticulate. Chromosome numbers: x=9, 10 for *S. nigricans*; other species unknown.

KEY TO SPECIES

1. Plants creeping, herbaceous, not woody or stems slightly woody toward base; Mexico, rare and disjunct. ——— **5. S. umbratilis**
1. Plants not creeping, stems or bases woody.

2. Plants shrublets or woody herbs, densely matted, prostrate, leaves overlapping; Coahuila, Mexico and Brewster Co., Texas. _____ **2. S. mullerae**
2. Plants not shrublets, woody at base or on lower stems, not densely matted, erect or spreading, leaves not or only slightly overlapping.
   3. Inflorescence very open and diffuse, leaves in inflorescence very small or lacking; Brewster Co., Texas. _____ **1. S. butterwickiae**
   3. Inflorescence not diffuse or if somewhat diffuse then having apparent leaves in inflorescence.
      4. Stem leaves narrowly lanceolate to ovate-lanceolate or somewhat elliptic, leathery, cuspidate, margins scabrid or ciliate; capsules subglobose; southwestern Texas and northern Coahuila. _____ **4. S. rupicola**
      4. Stem leaves various, not leathery, not cuspidate, margins not scabrid or ciliate; capsules longer than wide or subglobose only in *S. nigricans* var. *floridana*. _____ **3. S. nigricans**

1. Stenaria butterwickiae (Terrell) Terrell, comb. nov. (**Fig. 2**) *Houstonia butterwickiae* Terrell, Brittonia 31:164. 1979. *Hedyotis butterwickiae* (Terrell) Nesom, Syst. Bot. 13:434. 1988. TYPE: U.S.A. TEXAS: Brewster Co.: numerous in shallow pockets or crevices of limestone bedrock along ridgetop of Bullis Range, Bullis Gap Ranch, ca. 20 mi S of Sanderson, 2–3 mi NW of Rio Grande River, 29° 47' 30" N, 102° 32' 30" W, assoc. with *Penstemon baccharifolius, Phyllanthus ericoides, Polygala maravillasensis, Cirsium turneri*, 27 Aug 1977, *M. Butterwick, E. Lott, & S. Kennedy 3893* (HOLOTYPE: US!; ISOTYPES: GH! LL! MICH! MO! NY!). PARATYPE: Type locality, 16 May 1977, *M. Butterwick & E. Lott 3588* (LL!).

Perennial herb with a thick woody tap root and woody crown. Stems to 25 cm tall, often numerous, slender, wiry, glabrous, diffusely branched from upper nodes, the internodes longer than leaves, the nodes often tinged black. Basal leaves to 7 mm long, to 1 mm wide, somewhat clustered, sessile, linear, shorter, slightly wider, and thicker than cauline ones, glabrous; cauline leaves to ca. 20 mm long, 0.5–1 mm wide, sessile, rather rigid, stiffly erect, filiform or linear, acuminate at apex, glabrous or scaberulous, the midrib thick, the margin revolute. Stipules to 1 mm long and wide, scarious, whitish, subtriangular, acuminate or truncate. Inflorescence with small, few-flowered cymes, the pedicels to ca. 1 cm long, filiform, the inflorescence very diffuse, leaves lacking or greatly reduced, flowers heterostylous. Hypanthium glabrous; calyx lobes 0.8–3 mm long, ca. 1/2–3/4 as long as corolla tube, linear-lanceolate, with thick midribs, sharply acute or acuminate, stiffly erect. Corolla 2.3–4.7 mm long, funnelform, white with several dark nerves, glabrous externally; tube 1.3–3 mm long, gradually widened distally, densely puberulent within; lobes 1–1.7 mm long, 0.5–1 mm wide, ovate-lanceolate, puberulent within. Pin flowers with stigma lobes 0.3–0.5 mm long, exserted 0.5–1.5 mm beyond corolla throat, anthers 0.8-1 mm long, included, attached near midpoint or 3/4-point of corolla tube. Thrum flowers with anthers ca. 1 mm long, whitish, subsessile at sinuses of corolla lobes, stigmas included in tube. Mature capsules 1.5–2 mm long, equally wide, 1/2–3/4 inferior, dehiscing loculicidally, slightly or somewhat compressed, subglobose, glabrous, much exceeded by erect calyx lobes. Seeds ca. 10–26 per capsule, 0.4–0.7 mm

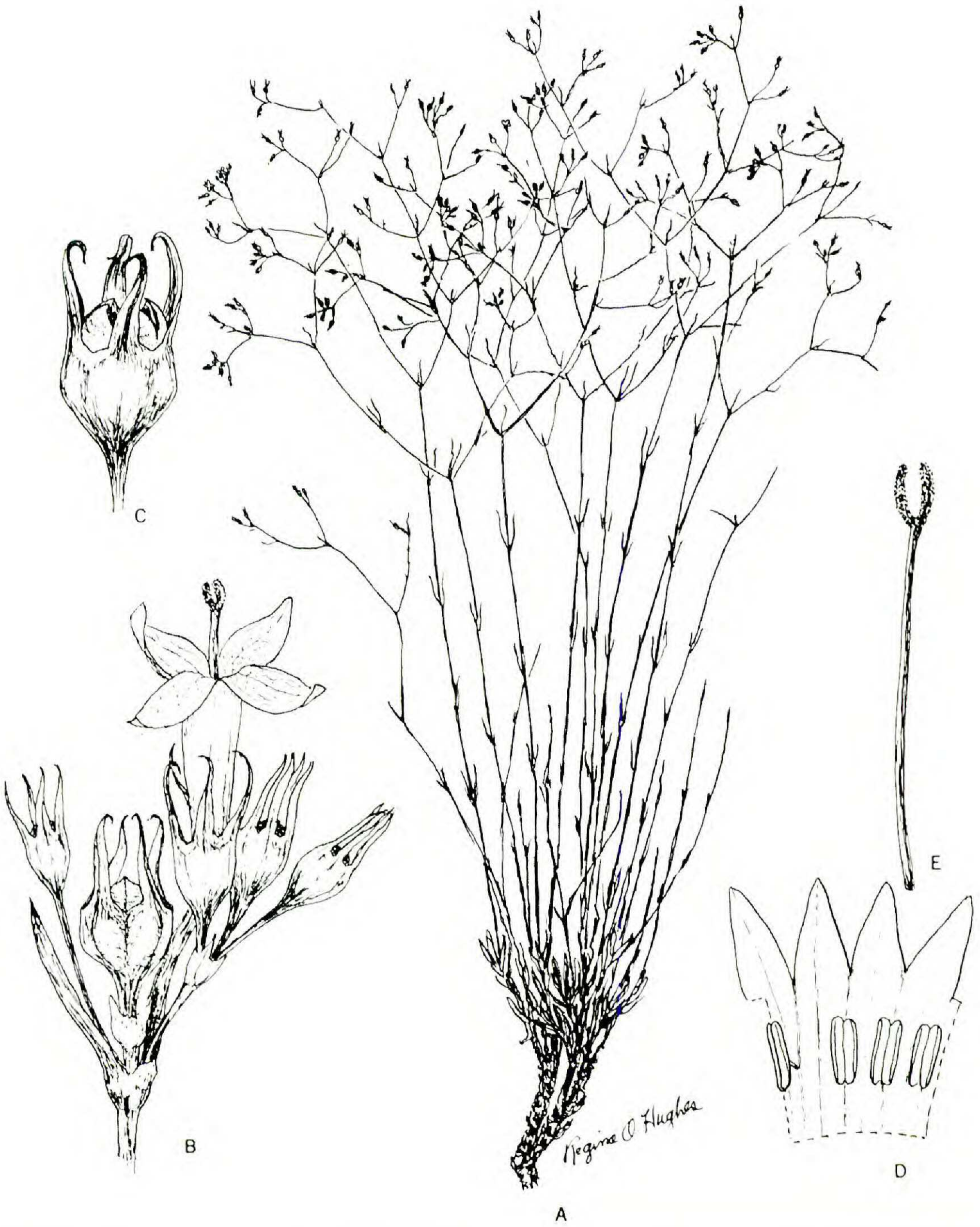

FIG. 2. *Stenaria butterwickiae*. Drawing of holotype reprinted from Brittonia 31:64. 1979. A. Habit, × .45. B. Detail of inflorescence, pin form, × 7. C. Capsule, × 5.5. D. Corolla with anthers, pin form, × 5.5. E. Style and stigma, × 5.5.

long, 0.3–0.4 mm wide, black or brown, ellipsoid, in outline elliptic or oblong, slightly or somewhat compressed, the hilum punctiform on ventral face, testa finely reticulate. Chromosome number unknown.

Phenology.—Flowering August.

Distribution.—Brewster Co., Texas. Known only from type collection.

Stenaria butterwickiae is distinctive in its very diffuse inflorescences without leaves or with leaves bract-like. The cauline leaves are small and stiffly erect. These characters are evident in Fig. 2.

2. Stenaria mullerae (Fosb.) Terrell, comb. nov. *Hedyotis mullerae* Fosb., Lloydia 4:288. 1941. *Houstonia mullerae* (Fosb.) Terrell, Brittonia 31:169. 1979. TYPE: MEXICO. COAHUILA: Mpio. de Cuatro Cienegas, Canon del Agua, Sierra de la Madera, 9 Sep 1939, *C.H. Muller 3234* (HOLOTYPE: US!, where transferred from NA; ISOTYPE: GH!).

Shrublets or perennial herbs, roots woody or with woody rhizomes to 6 mm thick. Stems to ca. 10 cm tall, often prostrate, matted, woody toward base, tetragonal, often obscured by the numerous small leaves, glabrous, internodes 1–5 mm long. Leaves 2–8(–10) mm long, 0.7–2 mm wide, sessile, thick, often gray-green, sometimes shiny, lanceolate, elliptic, narrowly elliptic, or oblanceolate, hispidulous to glabrous above, glabrous or with midrib hairs beneath, midribs often thickened and conspicuous below, margins thickened and revolute, conspicuously ciliate to scabrous, apices obtuse, acute, or apiculate. Stipules to ca. 2 mm long, adnate basally, deltate, margin often ciliate, apices 0.2–0.4(–2) mm long, acute, acuminate or apiculate. Inflorescence with flowers heterostylous, axillary, usually in groups of 3–5, subsessile or on pedicels to 1 mm long. Hypanthium hispidulous to glabrous; calyx lobes 1–2.5 mm long, lanceolate, oblanceolate, or spatulate, sometimes incurved, ciliate to glabrous, apices obtuse or acute. Corollas 2.5–6(–8) mm long funnelform, white, "sometimes tinged rose," hirtellous within distally; tube 2–4(–5) mm long, 0.7–1.2 mm wide at throat; lobes 1–3 mm long, 1–1.5 mm wide, ovate or lanceolate, densely pubescent to glabrous on inner faces, apices sometimes with hairs. Pin flowers with stigma lobes 0.2–0.4 mm long, broadly elliptic to linear, exserted on filiform styles to 2 mm beyond throat, anthers 0.8–1.4 mm long, sessile, partly exserted at throat. Thrum flowers with anthers 0.7–1.5 mm long, linear or oblong, "greenish blue," attached near or at sinuses, exserted on filaments 0.5–1 mm long, stigma included, styles to 2.5 mm long, glabrous. Mature capsules 1–2.2 mm long and wide, 1/2–4/5 inferior, compressed-subglobose, dehiscing loculicidally, apices broadly rounded or retuse. Seeds 0.6–0.8 mm long, 0.3–0.5 mm wide, black, rather shiny, somewhat compressed, in outline elliptic or angular-elliptic, hilum punctiform, on flat or slightly concave ventral surface, testa finely reticulate. Chromosome number unknown.

KEY TO VARIETIES OF *S. MULLERAE*

1. Leaves lanceolate, tapering gradually to a sharp point; stipules cuspidate with caudae 1–2 mm long. _____ 2b. var. **pooleana**
1. Leaves elliptic, narrowly elliptic, oblanceolate, or narrowly oblanceolate, obtuse, acute, or apiculate; stipules abruptly pointed, apiculate, or scarcely pointed, apical points 0.2–0.4 mm long. _____ 2a. var. **mullerae**

2a. Stenaria mullerae var. **mullerae** (**Fig. 3**).

Leaves 2–8(–10) mm long, usually gray-green, elliptic, narrowly elliptic, or oblanceolate, hispidulous to glabrous above, margins conspicuously ciliate to scabrous, apices obtuse, acute, or apiculate; stipules with apices scarcely pointed to abruptly short-pointed (more or less apiculate), apical points 0.2–0.4 mm long.

Phenology.—Flowering May to September.

Distribution.—Mexico: central (including Cuatro Cienegas Basin) and western Coahuila; rock crevices, steep slopes, ridge crests, cliff walls, usually on limestone, 1250–3000 m.

Selected representative specimens examined: **MEXICO. Coahuila:** ca. 35 km W of Cuatro Cienegas in Canyon de la Hacienda, Sierra de la Madera, near 27° 3' N, 102° 24' W, 7300 ft, *Henrickson & Wendt 11889* (ASU); ca. 31 air mi WNW of Cuatro Cienegas, Sierra de la Madera, S of Canyon Desiderio, 27° 06' N, 102° 32' W, 2700–2800 m, *Henrickson & Prigge 15275* (LL); SW end of Sierra de la Fragua, 1–2 km N of Puerto Colorado, *I.M.Johnston 8741* (GH, LL); W side of Potrero de la Mula, about 20 km NW of Ocampo, *I.M.Johnston 9245A* (GH); Sierra San Marcos, N part jutting into Cuatro Cienegas basin, 26° 47' – 26° 51' N, 102° 04' – 102° 07' W, 1250–1800 m, *M.C.Johnston et al. 10925* (LL, TEX, US); Mina El Aguirreño, N side of Sierra de la Paila, 26° 05' 30"– 06' N, 101° 36' W, 1700–2200 m, *M.C.Johnston et al. 11692* (LL); Sierra de San Marcos, opposite Los Fresnos, *Pinkava et al. P-6011* (ASU, ENCB, LL, NY).

Stenaria mullerae is variable in leaf size and shape, leaf vestiture, and compactness. Certain collections are somewhat intergradient with *S. nigricans*, suggesting possible hybridization.

2b. Stenaria mullerae var. **pooleana** (B.L. Turner) Terrell, comb. et stat. nov.

Hedyotis pooleana B.L. Turner, Phytologia 79:93. 1995. TYPE: U.S.A. TEXAS. Brewster Co.: Brushy Canyon Preserve (Nature Conservancy of Texas), Dead Horse Mountains (Sierra del Caballo Muerto), ca. 0.7 mi SW of adobe house on Brushy Canyon divide (29° 27' N, 102° 58' W), 4900 ft, N to E-facing vertical limestone cliff face, with *Agave lecheguilla, Rhus virens, Quercus pungens*, 1 May 1987, *Jackie Poole 2942* (HOLOTYPE: TEX!).

Leaves usually 5–7 mm long, lanceolate, bright green, glabrous, scabrous on margins, at apex tapering gradually into a long sharp point (more or less cuspidate). Stipules with long narrow caudae 1–2 mm long, sometimes irregularly toothed.

Phenology.—Flowering May.

Distribution.—United States. Texas, Brewster County. Dead Horse Mountains (Sierra del Caballo Muerto), 29° 27' N, 102° 58' W. Known only from type collection. Also seen by the collector (but not collected) about one mile from the type locality on 27 November 1987, along the same ridge at about 4840 ft elevation within the boundary of the Big Bend National Park.

Additional collection: Type locality, 25 May 1985, *Poole 2527* (SRSC, TEX!).

Turner (1995b) in the abstract of his paper described *H. pooleana* as closely related to *H. mullerae*, but differing in having lanceolate, markedly thickened leaves with glabrous surfaces and apiculate apices. In addition, he provided

FIG. 3. *Stenaria mullerae* var. *mullerae*. Part of holotype (US).

measurements of other organs. Terrell (1996b) advocated sinking of *H. pooleana* into *H. mullerae*, based on previous study of the considerably variable *H. mullerae* in loans from ASU, ENCB, GH, NY, TEX, and US. Turner (1997) defended specific status. Recently, I have re-examined specimens and types from US and TEX (on current loan) and I now advocate varietal status for *H. pooleana*.

There are two clear differences between the two taxa: in leaf shape and stipule shape. *Hedyotis pooleana* has lanceolate leaves which taper gradually to their tips, whereas in *H. mullerae* the leaves vary from elliptic or oblanceolate to narrowly elliptic or narrowly oblanceolate, with the apices varying obtuse, acute, or apiculate. (That Turner attributed apiculate apices to *H. pooleana* appears to have been a lapse.) I accept these terms more or less as pictured by Lawrence (1951, p. 744, Fig. 307). (Also, the leaves of *H. mullerae* range from densely pubescent to glabrous). Turner did not mention stipular differences, however, these are at least as well marked as the leaf characters: var. *mullerae* has stipules with very short, abruptly narrowed apices, whereas var. *pooleana* has stipules more or less cuspidate with narrow caudae 1–2 mm long.

I believe that these differences in vegetative characters represent varietal, rather than specific differences in the variable *S. mullerae*. The two varieties are about 150 miles apart. Turner (1995b) stated that the Dead Horse Mountains (Brewster Co., Texas) are an extension of the Sierra del Carmen range "across the Rio Grande in Coahuila." Thus, it seems possible that the two varieties may

have come from similar original stock, but have been isolated from each other for many millenia.

3. Stenaria nigricans (Lam.) Terrell, comb. nov. *Gentiana nigricans* Lam., Encycl. 2:645. 1788. *Houstonia nigricans* (Lam.) Fern., Rhodora 42:299. 1940. *Hedyotis nigricans* (Lam.) Fosb., Lloydia 4:287. 1941. TYPE: Herb. Jussieu (HOLOTYPE: P; photo, Fernald 1940).

Perennial herb with woody tap root to ca. 1.5 cm thick, foliage sometimes blackened when dried. Stems to 6.2 dm tall, often many-stemmed from broad woody base, stout to slender, erect, spreading, or decumbent, tetragonal and slightly winged, glabrous, scabridulous, papillose or densely puberulent or pubescent with gland-tipped hairs, occasionally with localized groups of densely aggregated white hairs. Leaves 7–40 mm long, 0.3–5(–8) mm wide, often fasciculate, sessile or tapering to short petioles, strongly revolute, filiform, linear, narrowly elliptic, elliptic, narrowly lanceolate, or narrowly oblanceolate, acute or obtusish, glabrous, scabridulous, densely puberulent or pubescent. Stipules to ca. 3.5 mm long and wide, scarious, deltate, ovate or lanceolate, sometimes acuminate or caudate, 0–few toothed. Inflorescence of few–many dense to loose cymes, often many-flowered (sometimes hundreds), flowers heterostylous, sometimes central or oldest flowers sessile or subsessile, other flowers on pedicels to ca. 10 mm long. Hypanthium glabrous to hirsute; calyx lobes 0.5–3(–4.4) mm long, 0.2–1 mm wide, slightly longer to slightly shorter than capsules, lanceolate or triangular-lanceolate, glabrous to hirsute, margins glabrous to ciliate, apices acute or mucronate. Corollas (2–)3.5–8.5 mm long, salverform to funnelform, quite variable in shape and size, white, light purple, pink, or lavender, buds elliptic, becoming obovate or oblanceolate and tapering to truncate or obtuse apices with or without hairs; tube (1.5–)2–4(–5.5) mm long, 0.4–1 mm wide at base, 0.5–2.5 mm wide at throat, often densely puberulent to hirsutulous within, tube length/lobe length ratio usually 1:1 to 2:1; lobes 4(–5), 1–3.5(–4.5) mm long, 0.5–2 mm wide, lanceolate or ovate, usually densely puberulent, pubescent, or hirsutulous on inner faces with white often gland-tipped hairs to ca. 0.6 mm long, apices also sometimes hairy. Pin form with stigmas bilobed, 0.3–1(–1.3) mm long, subglobose or broadly elliptic, papillose or pubescent, oblong, elliptic or linear, exserted to 3.5 mm beyond corolla throat on styles 4.5–5 mm long, anthers 4(–5), 0.8–1.8 mm long, linear or narrowly oblong, included at distal end of corolla tube or with tips exserted at corolla throat. Thrum form with 4(–5) anthers, 0.6–2.0 mm long, narrowly oblong or linear, usually blue or white, straight or curved, exserted on slender or flattened filaments ca. 0.5–2.5 mm long, attached near ends of anthers, stigmas ca. 0.3–0.8 mm long, included, linear, extended to near 2/3-point or to distal end of corolla tube on styles 1.5–2.5 mm long. Mature capsules 1.5–4.5 mm long, 1–2.7 mm wide, (1–)1.3–2 times longer than wide, (1/2–)3/4(–4/5) inferior, somewhat compressed, turbinate, obovoid or broadly ellip-

soid, quite variable in shape and size on an individual plant, glabrous or scabrous to hirsutulous, apices retuse, truncate, or broadly rounded, dehiscing widely loculicidally, then septicidally through septum, eventually forming two or four terminal segments. Seeds 0.45–1.15 mm long, 0.3–0.6 mm wide, black or dark brown, often shiny, somewhat compressed, ellipsoid, in outline elliptical, oblong, or slipper-shaped, ventral face with punctiform hilum more or less centered on flat, slightly concave, or slightly ridged surface, testa finely reticulate.

KEY TO VARIETIES OF *S. NIGRICANS*

1. Leaves more or less elliptic, 2.5–3.5(–4) times longer than wide; corollas usually 4-6 mm long; Mexico and southwest Texas _____ 3d. var. **gypsophila**
1. Leaves usually filiform, linear, narrowly lanceolate, or oblanceolate, more than 4 times longer than wide; corollas 2–8 mm long.
   2. Capsules subglobose, 1.2–2.5 mm long, 1.2–2.2 mm wide, 1–1.3 times longer than wide; leaves 0.2–1.2 mm wide; corollas 3–5(–6) mm long; southern Florida, Bahamas. _____ 3c. **var. floridana**
   2. Capsules longer than wide, 1.5–4.5 mm long, 1–2.7 mm wide, 1.3–2 times longer than wide; leaves 0.3–8 mm wide; corollas 2–8 mm long.
      3. Corollas 2–4(–4.5) mm long; leaves 0.7–2(–3.2) mm wide; Mexico. ____ 3b. var. **breviflora**
      3. Corollas (2.5–)3–8 mm long; leaves 0.3–8 mm wide; wide-ranging. ____ 3a. var. **nigricans**

3a. Stenaria nigricans var. **nigricans** (**Fig. 4**). *Houstonia angustifolia* Michx., Fl. Bor.-Amer. 1:85. 1803. Non *Hedyotis angustifolia* Cham. & Schlecht., 1829. *Oldenlandia angustifolia* (Michx.) A. Gray, Pl. Wright. 2:68. 1853. *Chamisme angustifolia* (Michx.) Nieuwl., Amer. Midl. Naturalist 4:92. 1915. *Hedyotis stenophylla* Torr. & A. Gray, Fl. N. Amer. 2:41. 1841. (*Houstonia angustifolia* listed as synonym). *Hedyotis lasiantha* Nutt. ex A. Gray, Pl. Wright. 1:81. 1852, as syn. of *H. stenophylla* Torr. & A. Gray, invalid name. (Specimens labelled *H. lasiantha* in BM, K, PH). TYPE: U.S.A. FLORIDA: "submaritimis Floridae" (HOLOTYPE: P!).

Houstonia rupestris Raf., Ann. Gen. Sci. Phys. 5:226. 1820. Non *Hedyotis rupestris* Swartz, 1797. TYPE: U.S.A. KENTUCKY: rocks bordering Kentucky River, specimen lost?

Oldenlandia angustifolia (Michx.) A. Gray var. *filifolia* Chapm., Fl. S. U.S. 181. 1860. *Houstonia angustifolia* Michx. var. *filifolia* (Chapm.) A. Gray, Syn. Fl. N. Amer. 1(2):27. 1884. *Houstonia filifolia* (Chapm.) Small, Fl. S.E. U.S. 1109, 1338. 1903, as "(A. Gray) Small." *Hedyotis nigricans* var. *filifolia* (Chapm.) Shinners, Field & Lab. 17:168. 1949. TYPE: U.S.A. "S. FLORIDA," *Chapman s.n.* (LECTOTYPE: US-83375! designated by Terrell 1986).

Houstonia angustifolia var. *scabra* S. Watson, Proc. Amer. Acad. Arts 18:97. 1883. *Hedyotis nigricans* var. *scabra* (S. Watson) Fosberg, Lloydia 4:288. 1941. TYPE: MEXICO. COAHUILA: Caracol Mountains 21 miles southeast of Monclova, 19-22 Aug 1880, *Palmer 410* (LECTOTYPE, here designated, GH!; ISOTYPES, LL! NY! PH! US! VT!). Isotype at LL designated by Turner 1995a.

Houstonia angustifolia var. *rigidiuscula* A. Gray, Syn. Fl. N. Amer. 1(2):27. 1884. *Houstonia rigidiuscula* (A. Gray) Wooton & Standley, Contr. U.S. Natl. Herb. 16:175. 1913. *Hedyotis nigricans* var. *rigidiuscula* (A. Gray) Shinners, Field & Lab. 17:168. 1949. SYNTYPES: "S. and W. Texas, *Palmer, Havard, & c.* Coast of E. Florida, *Rugel.* (Mex.)." Two sheets in GH include a possible lectotype.

Houstonia salina A. Heller, Contr. Herb. Franklin and Marshall Coll. 1:96, pl. 9. 1895.

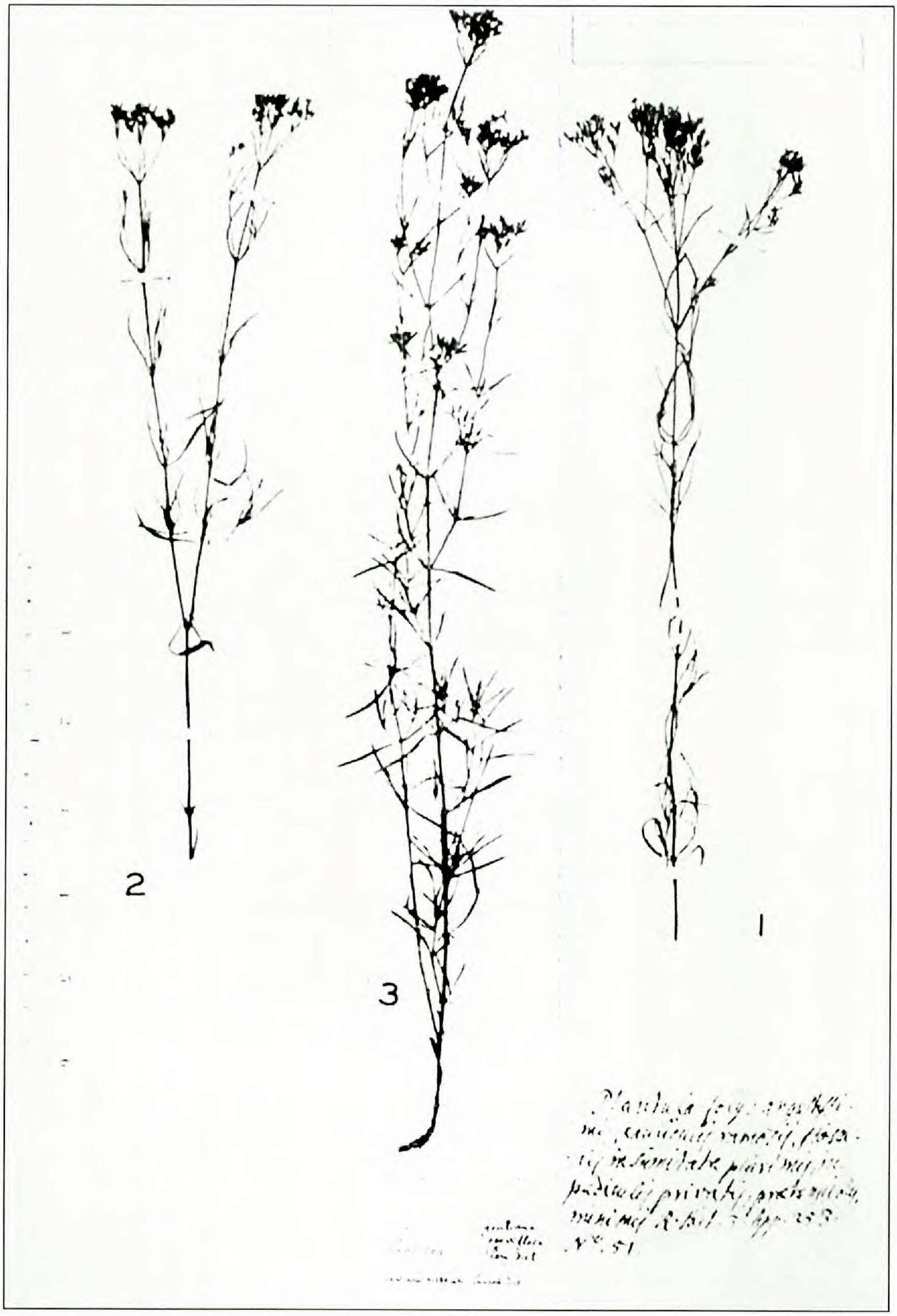

FIG. 4. Type of *Gentiana nigricans*, Paris herbarium, left and right plants. Middle plant is from Georgia, chosen by Fernald to show similarity with type. Plate 625 from Fernald 1940.

Hedyotis salina (A. A. Heller) Shinners, Field & Lab. 17:169. 1949. *Hedyotis nigricans* f. *salina* (A. Heller) W.H. Lewis, Rhodora 63:222. 1961. TYPE: U.S.A. TEXAS. Nueces Co.: shell deposit along beach, Corpus Christi, 31 May 1894, *A. A. Heller 1812* (LECTOTYPE designated by Terrell 1986, GH!; ISOTYPES, BM! ILL! K! MO! NY! PH! US-3!).

Houstonia pulvinata Small, Bull. New York Bot. Gard. 1:289. 1899. *Hedyotis nigricans* var. *pulvinata* (Small) Fosb., Castanea 19:37. 1954. *Houstonia nigricans* var. *pulvinata* (Small) Terrell, Phytologia 59:79. 1985. TYPE: U.S.A. FLORIDA. St. Johns Co.: sandy soil, St. Augustine, Jul 1876, *Mary C. Reynolds s.n.* (LECTOTYPE designated by Terrell 1986: NY!; ISOLECTOTYPE: NA!). PARALECTOTYPES, same locality and date, *A. P. Garber s.n.* (NY! US-2!).

Houstonia tenuis Small, Fl. S.E. U.S. 1109, 1338. 1903. TYPE: U.S.A. TEXAS. San Saba Co.: San Saba, Oct 1850 (?), *Thurber 67* (HOLOTYPE: NY!).

Hedyotis nigricans var. *austrotexana* B.L. Turner, Phytologia 79:15. 1995. TYPE: U.S.A. TEXAS: Karnes Co.: roadside 2 mi E of El Tejano Cafe, dry sandy clay soil, 22 June 1952, *Joe C. Johnson 833* (HOLOTYPE: LL).

Hedyotis nigricans var. *papillacea* B.L. Turner, Phytologia 79:15. 1995. TYPE: U.S.A. NEW MEXICO. Otero Co.: northern McKittrick Canyon at first crossing of Texas-New Mexico boundary, gravels and boulders of stream bottom, 8 Oct 1973, *Thomas F. Patterson 508* (HOLOTYPE: LL).

Leaves 0.3–8 mm wide, filiform, linear, narrowly lanceolate, or narrowly oblong, and more than 4 times longer than wide; corollas (2-5–)3–8 mm long; capsules 1.5–4.5 mm long, 1–2.7 mm wide, 1.3–2 times longer than wide.

Chromosome numbers.—Lewis (1959) reported $2n$=18 for var. *nigricans* from Nacogdoches Co., TX. Lewis (1962) listed n=9 for forma *salina* (San Patricio Co., TX), n=9 and 10 for var. *nigricans* (Chaves Co., NM and Brewster Co., TX) and n=10 for var. *rigidiuscula* (Brewster Co., TX). Lewis in Terrell et al.(1986) counted n=10 and $2n$=20 for var. *pulvinata* (St. Johns Co., FL). These varieties and the forma are here sunk under var. *nigricans*.

Common name.—diamond flowers.

Phenology.—Flowering usually April to December in Mexico; in U.S.A. usually April to October or all year in Florida.

Distribution.—United States. Southern Michigan (Branch Co.) and Ohio south to Florida, west to Iowa, Nebraska, eastern Colorado, and New Mexico; Mexico: Sonora, Chihuahua, Coahuila, Nuevo León, Tamaulipas, San Luis Potosí, and Hidalgo.

Selected representative specimens examined: **MEXICO. Chihuahua:** Sierra Grande, 3 km E of Rancho El Murcielago, 29° 52' N, 104° 50' W, *M.C. Johnston et al. 11293* (CAS, TEX). **Coahuila:** 8 km S of El Tule, 24 km N of Castillon, *Stewart 441* (CAS, GH, MO). **Nuevo León:** 7 mi W of Iturbide along hwy 60, *McGregor et al. 32* (KANU, NY, SMU, US).

UNITED STATES. ALABAMA. Dallas Co.: roadbank 9 mi W of Selma, *Webster & Wilbur 3508* (FLAS, MICH, NCSC). **ARKANSAS. Clark Co.:** Arkadelphia, *Demaree 15643* (FLAS, NY, TENN). **Garland Co.:** Hot Springs, *Harvey 12824* (IA, KANU, MICH). **COLORADO. Yuma Co.:** 0.75 mi S of Laird, *McGregor 32365* (KANU). **FLORIDA. Franklin Co.:** 6 mi NE of Alligator Point, *Kral 2800* (FLAS, FSU). **GEORGIA. Decatur Co.:** along Flint River 1 mi N of Chattahoochee, Florida, *Thorne 5931* (GA, IA, MICH, MT). **ILLINOIS. Jersey Co.:** Pere Marquette State Park, *Evers 25019* (ILLS). **INDIANA. Harrison Co.:** 1 1/2 mi NE of Davidson, *Deam 37238* (IND). **IOWA. Fremont Co.:** Hamburg, *Shimek s.n., 31 Aug 1898*, (IA). **KANSAS. Montgomery Co.:** 3 mi S of Independence, *Horr E256* (ASU, CM, FLAS, ISC, KANU, MT,

NCSC, NO). **KENTUCKY. Wayne Co.:** Beaver Creek SW of Monticello, *Smith & Hodgdon 3907* (GH). **LOUISIANA. Caddo Parish**: 3 mi S of La. 526 at Forbing, *Thomas & Dorris 96086* (KANU, WNC). **MICHIGAN. Branch Co.:** loc. not given, *Mrs. J.M. Mulligan s.n., Jun 1889* (US). **MISSOURI. Franklin Co.:** 3 mi S of Grays Summit, *Steyermark 601* (MO). **NEBRASKA. Cass Co.:** Weeping Water, *Sheldon s.n., 17 Aug 1898* (WVA). **NEW MEXICO. Lincoln Co.:** 15 mi E of El Capitan, 8500 ft, *Hitchcock et al. 4239* (ISC, NO). **OHIO. Ottawa Co.:** Rattlesnake Island, *Moseley s.n., 29 Jul 1895* (CM, F, MICH, MO). **OKLAHOMA. McClain Co.:** 3 mi E of Blanchard, (Pl. Exs. Grayanae 686), *Demaree s.n., 30 Jun 1936* (DUKE, GA, IA, ISC, KANU, MICH, MT, NCSC, NO, PAC, TRT, WIS, WVA). **TEXAS. Kerr Co.:** Kerrville, *Heller 1661* (ARIZ, IA, MICH). The preceding citation of specimens lists one specimen from most states of the United States where the typical variety occurs. Only a few Mexican specimens were cited because of lack of detailed notes on morphology. Turner (1995a) provided a map of the Texas distribution.

Previous to 1940 the name *Houstonia angustifolia* Michx. was usually applied to the species later known as *Hedyotis nigricans*. Fernald (1940, plate 625) presented an illustration of the type of *Gentiana nigricans* Lamarck from the Paris herbarium (shown here as Fig. 4). Fernald's plate shows two plants of the type collection along with a plant from Georgia collected by Boykin near the type region of *Houstonia angustifolia*. The three plants are very similar, so much so that Fernald commented "That they are the same no one is likely to question." The plants of the type collection are tall, rather strict, linear-leaved, and generally similar to other plants from the southeastern United States.

Stenaria nigricans is a polymorphic species. Plants from Adams County in southern Ohio are short and decumbent; plants from the southeastern U.S.A. often are tall and have very narrow leaves; plants from Kansas and Nebraska are often very stout and large, with thick, broad, woody bases and heavy taproots. Plants may also differ conspicuously from one population to another in size of corollas. This is only a small example of the variation, much of which seems to occur at random. I have not studied *S. nigricans* in detail, and leave it to future workers to study the species in depth.

Certain varieties are here placed in synonymy. Variety *scabra* S. Watson is only a hairier-than-average extreme connected with the typical plants by a continuum. Variety *rigidiuscula* A. Gray is a confused and ambiguous name whose protologue seems to refer to more or less typical plants of *S. nigricans*; the specimens cited as syntypes came from Texas and Florida and are rather diverse. Turner (1995a) came to a similar conclusion about this variety.

Houstonia salina and *H. tenuis* were discussed previously by Terrell (1986). I concluded that they did not merit varietal status. Turner (1995a) agreed with this conclusion.

Terrell (1986) compared var. *pulvinata* with var. *nigricans*, and maintained the former as a variety. Further consideration, however, leads me to conclude that its differences overlap so strongly with those of var. *nigricans* that it should be in synonymy.

Turner's (1995a) var. *austrotexana* and var. *papillacea* appear to differ from

var. *nigricans* in rather minor ways, considering the great amount of variation in *S. nigricans*; e.g., var. *austrotexana*: "Resembling var. *nigricans* but the more mature calyces markedly papillose throughout." Variety *papillacea* is also papillose and appears to be delimited by the Texas border. I examined specimens of both varieties lent to me from TEX and specimens available in BRIT, but I could not accept their being sufficiently distinct to recognize as varieties (Terrell 1996b). Turner (1997) again upheld these varieties. *Stenaria nigricans* is an exceedingly variable entity, and I find it somewhat premature to recognize varieties on minor vestiture characters in Texas without studying the species in Oklahoma and throughout its range.

3b. Stenaria nigricans var. **breviflora** Terrell, var. nov. TYPE: MEXICO. NUEVO LEÓN: Sierra Madre near Monterrey, *C.G. Pringle 13878* (HOLOTYPE: US!; ISOTYPES: CAS! F! GH! MEXU! MICH! MO! MSC! SMU! VT!).

Folia saepe 0.7–2(–3.2) mm lata, linearia vel filiformia; corollae 2–4(–4.5) mm longae; capsulae 1.8–3(–3.8) mm longae. 1.3–2.2 mm latae, 1–1.5(–2) plo longiores quam latiores.

Leaves usually 0.7–2(–3.2) mm wide, linear or filiform; corollas 2–4(–4.5) mm long; capsules usually 1.8–3(–3.8) mm long, 1.3–2.2 mm wide, 1–1.5(–2) times longer than wide, often glabrous.

Distribution.—Mexico: Nuevo León, vicinity of Monterrey, and in adjacent Coahuila. I have 30 records of this variety from 15 herbaria. The habitats are variously: limestone (travertine) and talc-like soil on gravelly hill; rocky limestone valley; sandy loam; dry pine-oak forest; crevices of limestone rock; gypsum plug (of Portrero Chico); bottom of arroyo.

Selected representative specimens examined: **MEXICO. Coahuila:** Ojo Caliente, 33 mi SW of Monterrey, *Warnock & Barkley 14744M* (ENCB, F, GH, MO, NY, TEX). **Nuevo León:** 5 km S of Sabinas Hidalgo on road to Monterrey, *Frye & Frye 2408* (GH, NY, US); 16 mi SW of Villa Santa Catarina, *Hernandez C. et al. 16M516* (TEX); Diente Canyon, Monterrey, *Muller & Muller 111* (F, GH, MEXU, TEX); toll road up Sierra Anahuac, 4.5 mi SE of Monterrey, *Oliver 202*, (SMU, TEX, US); 25 km NW of Monterrey, Portrero Chico, *Powell & Turner 2335* (TEX); between Linares and Galeana, 2500 ft, *Sharp 45653* (GH, TENN, US).

The main distinguishing character of this variety is the consistently short corollas. Also, the leaves are short and linear or filiform.

3c. Stenaria nigricans var. **floridana** (Standl.) Terrell, comb. nov. *Houstonia floridana* Standl., N. Amer. Fl. 32(1):36. 1918. *Hedyotis purpurea* var. *floridana* (Standl.) Fosb., Castanea 19:36. 1954. *Houstonia nigricans* var. *floridana* (Standl.) Terrell, Phytologia 59:79. 1985. *Hedyotis nigricans* var. *floridana* (Standl.) Wunderlin, Sida 11:400. 1986. TYPE: U.S.A. FLORIDA. Dade Co.: Cocoanut Grove, Biscayne Bay, Jul 1895, *A.H. Curtiss 5484* (HOLOTYPE: US!; ISOTYPES: FLAS! ISC! NY! US! VT!).

Stems usually 1–3.5 dm tall, sprawling, spreading, or erect, wiry and diffusely branched. Leaves filiform or linear, 0.2–1.2 mm wide. Corollas 3–5(–6) mm long, glabrate to densely pubescent within. Mature capsules subglobose, 1.2–2.5 mm long, 1.2–2.2 mm wide, 1–1.3 times longer than wide. Chromosome numbers:

Lewis (1962) reported n=9 for this variety (listed as var. *filifolia*) from Dade Co., Florida. Lewis in Terrell et al. 1986 reported n=9 and $2n$=18 for another collection from Dade Co., Florida.

Distribution.—Southern Florida: over limestone at a number of locations in Dade County, and at Big Pine Key in Monroe County; Bahamas: Grand Bahama Island, Great Abaco Island.

Selected representative specimens examined: **BAHAMAS. Grand Bahama Island:** Intersection of Settlers Way and Balao Road, Freeport, *Correll 440470* (NY); Buckingham-Leicester Co. line, Government Road, *Lewis 7182* (FSU, FTG, MO, NY). **Great Abaco Island:** halfway between Marsh Harbour and Marsh Harbour Airport, *Wunderlin et al. 8564* (USF).

UNITED STATES. FLORIDA. Dade Co.: Long Pine Key, *Brass* 32997 (USF); jct. Krome Ave., Moody Drive, 2 mi N of Homestead, S36, T56S, R38E, *Burch et al. 285* (FLAS); Pine Island, 25 mi S of Miami, E of Naranja and Homestead, *Elder* 289 (DUKE); 5 mi S of Florida City on US1, *C. & J. Janish 418* (CAS); 6 mi E of Royal Palm Park, *O'Neill 7584* (ARIZ, CAS, CM, MICH, MT, NO, US); Sykes Hammock, everglade keys, *Small, Mosier, & Small 6755* (CAS, DUKE, FLAS, MICH, US, WVA). **Monroe Co.:** Big Pine Key, *Brumbach 9392* (FSU); N of upper E-W road, Big Pine Key, *Killip 40896* (NO); 4 mi N of US1, Big Pine Key, *McDaniel 5813* (FSU).

Terrell (1986) discussed var. *floridana* and var. *filifolia* in detail, and concluded that the latter variety was a synonym of var. *nigricans*, as its description referred to plants unlike var. *floridana*.

Variety *floridana* is distinguished by having subglobose capsules. Because of these capsules Fosberg named it as *Hedyotis purpurea* [=*Houstonia purpurea*] var. *floridana*, but it has non-crateriform seeds like those of var. *nigricans* and does not belong in *Houstonia*.

3d. Stenaria nigricans var. **gypsophila** (B.L. Turner) Terrell, comb. nov. *Hedyotis nigricans* var. *gypsophila* B.L. Turner, Phytologia 79:15. 1995. TYPE: MEXICO. NUEVO LEÓN. Santa Rita, 2370 m, sparse pine woods, gypsum hillsides, 11 Jun 1981, *Hinton et al. 18278* (HOLOTYPE: TEX).

This new variety was described by Turner as follows: "Resembling var. *nigricans* but the plants low and much-branched from the base, the leaves elliptic-ovate and mostly 2.5–3.5(–4) times as long as wide (vs. linear-lanceolate to linear-oblanceolate, mostly 4–20 times as long as wide) and the mature calyces usually markedly hispid with broad-based hairs (vs. glabrous or merely minutely setose)."

My description incorporates items from Turner's description.

Stems woody at base, 0.4–2.5 dm tall. Leaves 4–17 mm long, 1–4(–6) mm wide, 2.5–3.5(–4) times longer than wide, elliptic or narrowly elliptic. Corollas usually 4–6 mm long. Capsules usually 2.5–3.2 mm long, 1.5–2.2 mm wide. Seeds 0.45–0.75 mm long, 0.3–0.6 mm wide.

Chromosome number.—Lewis (1962) listed n=9 under the name *H. nigricans* var. *angulata* (=*S. rupicola*), but the specimen was actually *S. nigricans* var. *gypsophila*.

Distribution.—Mexico: Northern and southeastern Chihuahua and northern Coahuila south southeast to Nuevo León, northeast Zacatecas, southwest

Tamaulipas, and San Luis Potosí. It has been much collected from the Saltillo and Galeana areas. The altitudes range from ca. 1500 to 3195 m. United States: Texas: Culberson, Hudspeth, and Jeff Davis counties. The specimens resemble Mexican collections, and this extends var. *gypsophila* northward into the United States. The range of habitats of the Mexican specimens includes the following: pine and oak forests; pinyon-juniper; pine-douglas fir; steep limestone slope; east-facing ravine; rocky slope; bank of dry arroyo; steep igneous slope; and gypsum flats in pine-pinyon.

The most conspicuous character is the elliptic leaves on rather small plants. As noted (Terrell 1996b) I was aware of this taxon prior to its description by Turner. Like Turner, I can not find any other characteristics significantly different from var. *nigricans* (hairy mature calyces occur in var. *nigricans*). I consider the taxon as misnamed, as I recorded only one collection out of 49 Mexican collections from 19 herbaria that mentioned a gypsum substrate. It may be noted that the type specimen came from a gypsum habitat.

Plants superficially somewhat resemble those of some variants of *Houstonia longifolia*, which occurs in the eastern and central U.S.A. (Terrell 1996a). Variety *gypsophila* may also be confused with the Mexican species *Houstonia wrightii*. The latter species may occasionally occur at higher elevations near var. *gypsophila*, and a very few collections have had both species on one sheet. The following comparison may provide a means of distinguishing them: capsules of var. *gypsophila* are somewhat compressed, longer than wide, and eventually dehisce widely into four similar segments; seeds are ellipsoid with the hilum more or less centered on the ventral side and punctiform; buds often have hairy apices. *Houstonia wrightii* capsules are subglobose, not or only slightly compressed, wider than long; seeds have a linear hilar ridge in a ventral depression; bud apices are glabrous (Terrell 1996a).

Selected representative specimens examined: **MEXICO. Chihuahua:** Sierra de la Parra, across Rio Grande from Sierra Vieja, 1450–2158 m, 30° 00–02' N, 104° 52–53' W, *M.C.Johnston et al. 11314B* (TEX, US). **Coahuila:** 22 km ESE of La Cuesta del Plomo on Muzquiz-Boquillas hwy near intersection of hwy from V. Acuña, 1000 m, 28° 38' N, 102° 18' W, *Chiang et al. 7550R* (CAS, TEX, US); about 35 mi E of Saltillo, 5–6 mi E of Los Lirios, 2300–2400 m, *McVaugh 12338* (MICH); mpio. Villa Ocampo, Canyon de la Vaca, Sierra Santa Fe del Pino, *Passini & Robert 5193* (ENCB); Sierra Guadelupe, S of La Cuchilla, 2300–2600 m, *Pennell 17388* (F, PH, US). **Nuevo León:** Cañon del Voladero, Galeana, 2200 m, *Hinton 18744* (ASU, US); Cerro Potosí, near microwave tower, 9000 ft, *McGregor et al. 351* (TEX, US); mpio. Berrumbadero, Cañon de las Capulines above San Enrique Hacienda, San Jose de Raices, *Mueller 2413* (F, GH, MICH, MO). **San Luis Potosí:** 21.6 mi SE of San Luis Potosí, hwy 86 to Rio Verde, 7500 ft, *Oliver 190* (MO, SMU). **Tamaulipas:** 3 mi N of Miquihuana, *Stanford et al. 2399* (DS, US). **Zacatecas:** Sierra del Astillero, 24°34' N, 101° 04' W, *M.C.Johnston et al. 11557* (CAS, TEX, US).

UNITED STATES. TEXAS. Culberson Co.: south fork of McKittrick Canyon, Guadeloupe Mts., *Correll & Hanson 29822* (FSU, TEX); Victoria Canyon, E margin of Sierra Diablo, 1330–1700 m, 31° 20–21' 30" N, 104° 53–55' W, *M.C.Johnston et al. 10695* (TEX). **Hudspeth Co.:** Victoria Canyon, 1 mi from McAdoo Ranch, Diablo Mts., *Muller 8219* (MICH). **Jeff Davis Co.:** Davis Mts., Madera Canyon, *Webster 4501* (MICH).

4. **Stenaria rupicola** (Greenman) Terrell, comb. nov. (**Fig. 5**).*Houstonia rupicola* Greenman, Proc. Amer. Acad. Arts 32:286. 1897, non *Hedyotis rupicola* Sonder in Harvey & Sonder, Fl. Cap. 3:12. 1865. *Hedyotis stenophylla* Torr. & A. Gray var. *parviflora* A. Gray, Pl. Wright. 1:81. 1852, non *Hedyotis parviflora* Walpers, Ann. Bot. Syst. 2:772. 1852, nec *Houstonia parviflora* Holzinger ex Greenman, Proc. Amer. Acad. Arts 32:284. 1897. *Hedyotis angulata* Fosb. in Shinners, Field & Lab. 17:166, nom. nov. for var. *parviflora* 1949. *Hedyotis nigricans* var. *angulata* (Fosb.) W.H. Lewis, Amer. J. Bot. 49:865. 1962, nom. superfl. *Hedyotis nigricans* var. *parviflora* (A. Gray) W.H. Lewis, Ann. Missouri Bot. Gard. 55:32. 1968. TYPE: U.S.A TEXAS: Expedition from W. Texas to El Paso, N.M., May-Oct 1849, *C. Wright 238* (LECTOTYPE designated by Lewis (1968): GH!; ISOTYPES: GH! NY! PH! US!).

The protologue states "Crevices of rocks on the San Pedro River; July." The lectotype has atypical plants; the isotype at US has plants that are more typical. The San Pedro River is now the Devils River and is near Del Rio, Texas.

Small perennial herbs with woody taproots becoming 1 cm thick. Stems 2–15(–22) cm tall, sometimes many, quadrangulate, stiffly erect or ascending from thick (to 1 cm), woody, branched base, glabrous (sometimes shiny), scabrous, or pubescent on angles. Leaves 2–8(–12) mm long, 0.8–2(–2.5) mm wide, usually 3–6 times longer than wide, numerous, sessile, narrowly lanceolate to ovate-lanceolate or elliptic, thick, leathery, rigidly ascending or spreading, often shiny, cuspidate, glabrate, margin scabrid or ciliolate, midrib conspicuous beneath. Stipules 0.5–3 mm long, usually with linear or awl-shaped cauda, margins entire or toothed or ciliolate, teeth sometimes branched. Flowers heterostylous, in terminal, few-flowered cymes, pedicels to ca. 3 mm long. Hypanthium glabrous to pubescent or ciliate; calyx lobes 0.7–2.3 mm long, less than 0.5 mm wide, ovate-lanceolate or lanceolate, acute to subcaudate, rigidly erect, with thick dorsal rib, slightly to somewhat surpassing the mature capsules. Corollas 3.5–6 mm long, funnelform, white, buds obovate, often with apical hairs; tubes 2–3.8 mm long, ca. 0.8–1 mm wide at throat, puberulent or pubescent within; lobes 1–2.5 mm long, 0.7–1 mm wide, lanceolate or ovate, densely pubescent on inner faces, sometimes with hairs on apex. Pin flowers (predominating in herbarium specimens) with stigma lobes 0.3–0.8 mm long, oblong, stigmas exserted 1–2 mm beyond corolla throat, styles minutely puberulent, anthers located just below corolla sinuses. Thrum flowers with anthers 0.8–1.2 mm long, oblong or appearing subglobose, straight or curved, on filaments 0.5–1 mm, exserted to 1 mm beyond throat, stigmas located near midpoint of corolla tube. Mature capsules 1–2 mm long and wide, slightly longer than wide or subequal, 1/2–3/4 inferior, subglobose or slightly compressed, glabrous to pubescent. Seeds several–14 per capsule, 0.3–0.7 mm long, 0.25–0.5 mm wide, black or dark brown, shiny, ellipsoid, slightly to somewhat compressed, sometimes twisted or angular, ventral face with punctiform hilum, testa finely reticulate. Chromosome number unknown. Lewis (1962) listed *n*=9 for *Oliver 197* (MO, SMU, TEX) from Nuevo Leon as *H. nigricans* var. *angulata* (= *S. rupicola*); however, this collection

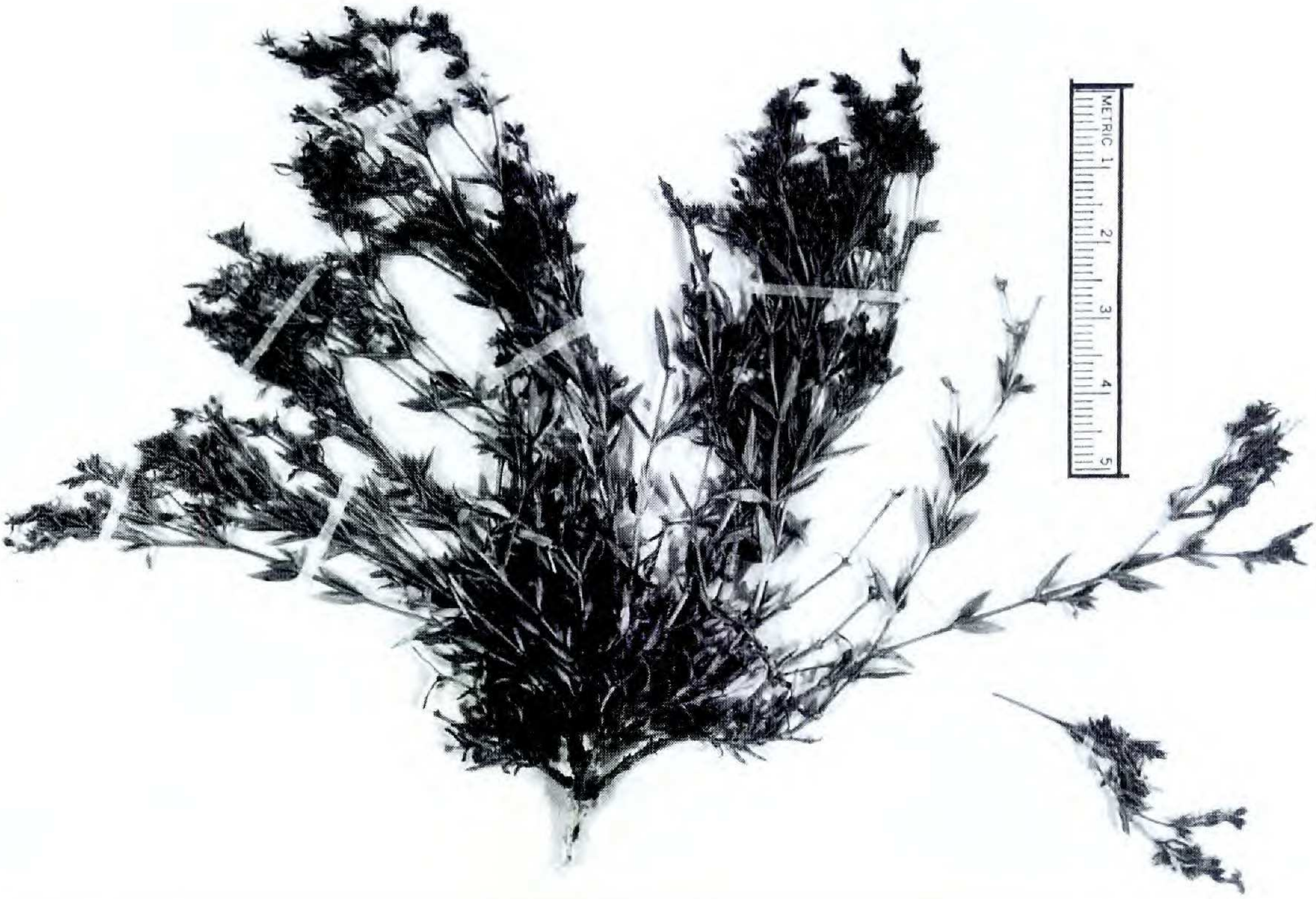

FIG. 5. *Stenaria rupicola*. *C.R. Orcutt 753* (US), Sanderson, Texas, 26 Jun 1924.

is not *S. rupicola* but *S. nigricans* var. *gypsophila*. *Stenaria rupicola* occurs no farther east than Coahuila.

Phenology.—Flowering May–November.

Distribution.—Rock crevices, talus slopes, gravelly soil, often over limestone, 500–2000 m (1500–6000 ft). United States: Southwestern Texas (Brewster, Crockett, Pecos, Presidio, Terrell, and Val Verde counties); also Culberson (atypical); Mexico: northern Coahuila in the Muzquiz area and northwest toward Boquillas del Carmen.

Selected representative specimens examined: **MEXICO. Coahuila:** 1 mi N of "La Laguna," Canyon del Mulato, Serranias del Burro, about 65 mi NW of Sabinas, 3500 ft, *Gould 10584* (ENCB, MICH); S. Paila (Valley Seco), G. Cepeda, *Hinton et al. 16540* (GH, NY, US); 140.3 km NW of Muzquiz on Hwy 53 towards Boquilla del Carmen, *Peterson & Annable 10595* (US); camp below Pichache de Centinela about 15 mi, 4600 ft, *Warnock 11538* (MICH, SMU).

UNITED STATES. TEXAS. Brewster Co.: 7 mi E of headquarters, Black Gap Wildlife Refuge, Maravillas Canyon, *D.S. & H.B.Correll 35355* (LL). **Crockett Co.:** Salviastrum Mesa, 32 airline mi NW of Ozona, *Cory 44377* (TEX). **Pecos Co.:** 40 mi S of Ft. Stockton on Sanderson Road, *Hinckley 4837* (US); main canyon on NE side of Sierra Madera, 25 mi S of Ft. Stockton, 1300 m, *McVaugh 10646* (MICH). **Presidio Co.:** Capote Canyon, 9 mi NE of Candelaria, *Ohlendorf 471* (LL). **Terrell Co.:** 1 mi E of Sanderson, 2885 ft, *Warnock 11885* (LL).

This species has been treated by me in the past as *Hedyotis angulata*, however, under *Stenaria* the earlier epithet, rupicola, may be used. It is quite distinct in leaf characters. Some collections are somewhat atypical, possibly due to introgression from *S. nigricans*. The species intergrades with *S. nigricans* and possibly with *S. mullerae*.

5. Stenaria umbratilis (B.L. Robinson) Terrell, comb. nov. *Houstonia umbratilis* B.L. Robinson, Proc. Amer. Acad. Arts 45:401. 1910. *Hedyotis umbratilis* (B.L. Robinson) W.H. Lewis, Rhodora 63:222. 1961. TYPE: MEXICO. NUEVO LEÓN: cliffs of mountains near Monterrey, 25 Apr 1906, *C.G. Pringle 13877* (HOLOTYPE: GH!; ISOTYPES: CAS! MEXU-2! MICH! MO! MSC! SMU! US! VT!).

Perennial herb. Stems prostrate, creeping, slender, glabrous or pubescent at nodes, rooting at some nodes. Leaves 2–5.5 mm long, 1–3 mm wide, subsessile or with petioles to ca. 1.5 mm long, 1-nerved, ovate or broadly elliptic, glabrous or pubescent above, glabrous and slightly paler below, acute or obtuse. Stipules minute, glabrous or sparsely pubescent, margins with one or more teeth or glands. Inflorescence with flowers solitary, axillary or terminal, on more or less straight pedicels to 3 mm long (var. *brevipedicellata*) or on slender deflected pedicels 3.5 to ca. 16 mm long, subtended by one or two bracts or leaves, flowers apparently homostylous. Hypanthium glabrous; calyx lobes 0.8–1.5(–2) mm long, 0.5–0.7 mm wide, erect, ovate-lanceolate, acutish or obtuse. Corollas 4.7–9 mm long, funnelform, white; tube 3–5 mm long, 0.5–1 mm wide at base, 1–3 mm wide at throat; lobes 1.5–4.2 mm long, 1.0–2.2 mm wide, ovate, spreading, puberulent or glabrate within. Anthers 0.6–1 mm long, 0.2–0.3 mm wide, narrowly oblong or oblong, filaments 0.5–2 mm long, somewhat exserted. Stigma lobes ca. 0.5 mm long, included in corolla tube. Mature capsules 1–2 mm long and wide, 1/2–3/4 inferior, subglobose, thin-walled, dehiscing widely loculicidally. Seeds 0.5–0.8 mm long, 0.3–0.6 mm wide, black, shiny, somewhat compressed, ovoid or ellipsoid, hilum centric, punctiform, testa finely reticulate. Chromosome number unknown.

The creeping habit of this species differs markedly from that of the other species of *Stenaria*; however, the ellipsoid seeds led me to place it with the other species of this genus. The typical variety has long pedicels that are deflected at an angle, whereas var. *brevipedicellata* consistently has short, more or less straight pedicels. The presently known distribution indicates separate ranges. The seeds of the two varieties are similar.

KEY TO VARIETIES OF *S. UMBRATILIS*

1. Stems often densely leafy because of the very short internodes; leaves somewhat leathery, revolute; flowers on more or less straight pedicels ca. 1–3 mm long. _____ 5b. var. **brevipedicellata**
1. Stems not densely leafy, internodes longer; leaves thin; flowers on long (3.5–16 mm), deflected pedicels. _____ 5a. var. **umbratilis**

5a. Stenaria umbratilis var. **umbratilis** (**Fig. 6**).

Leaves thin; flowers on long, deflected pedicels.

Phenology.—Flowering April, May.

Distribution.—Mexico: Nuevo León (near Monterrey), Veracruz (mpios. of Atzalan and Jalacingo). Rare and disjunct.

Additional specimens examined: **MEXICO. Veracruz:** orilla de arroyo, 800 m, Guatemimolo, mpio. de Atzalan, 13 Apr 1970, *F. Ventura A. 902* (US); orilla de arroyo, 1265 m, Agua Puente, mpio. de Jalacingo, 17 May 1972, *F. Ventura A. 5380* (US).

These collections have terminal or pseudoterminal flowers on rather long pedicels. In April, 1972, I searched unsuccessfully for this species in Diente Canyon, a few miles south of Monterrey. This canyon may have been the type locality. Seepage areas in this canyon are said to be drier than in Pringle's time.

5b. Stenaria umbratilis var. **brevipedicellata** Terrell, var. nov. (**Fig. 7**). TYPE: MEXICO. COAHUILA: steep-sided limestone mountains, calcareous gravel, Cañon de la Gavia south of Rancho de la Gavia, 1250–2200 m, 26° 18' 30"–20' N, 101° 15'–18' W, 2–3 Aug 1973, *M.C. Johnston, T.L. Wendt, F. Chiang, D. Riskind 12032B* (HOLOTYPE: US!; ISOTYPE: LL!).

Pedicelli 1–3 mm longi.

Leaves somewhat leathery, thickish; capsules on pedicels 1–3 mm long.

Distribution.—Mexico: Coahuila.

Additional collections: **MEXICO. Coahuila.** Mina El Aguirreño, N side of Sierra de la Paila, crevice plant, very steep slopes of limestone sierra, calcareous gravel, 1700–2200 m, 26° 05' 30"– 26° 06' N, 101° 36' W, 5 July 1973, *M.C. Johnston, T.L. Wendt, and F. Chiang C. 11681G* (LL); Mpio. Villa Acuña: Rancho El Rincón, on SW margin of Serranias del Burro (part of Sierra del Carmen), 1400–2100 m, 28° 40' N, 102° 15' W, ca. 80 km SE of Big Bend National Park, Texas, 28 May 1993, *Sandra Aguilar Ruiz 320 with Diana L. Doan-Crider* (TEX).

This variety has axillary flowers on short pedicels, compared with the long deflected pedicels of var. *umbratilis*.

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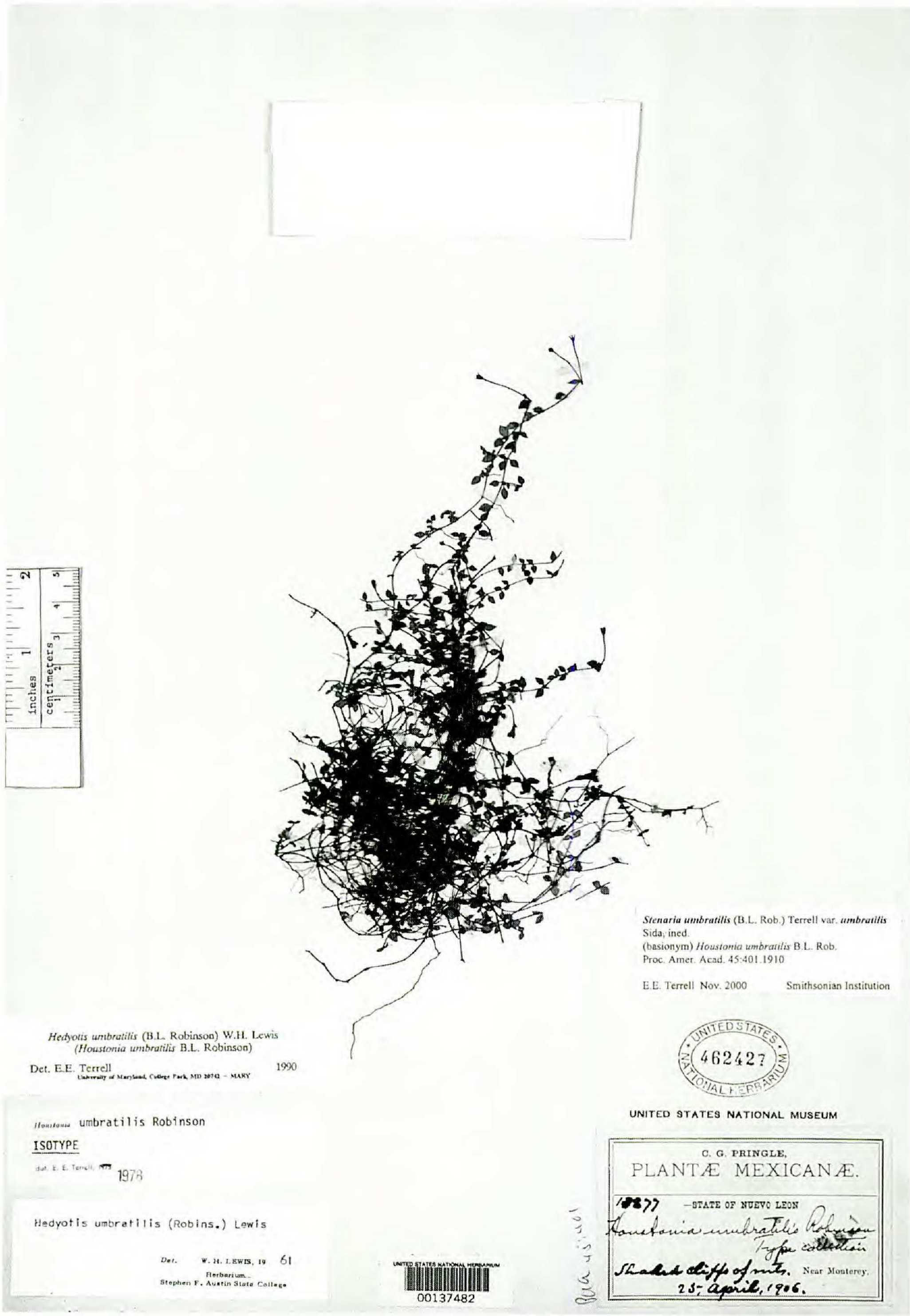

FIG. 6. *Stenaria umbratilis* var. *umbratilis*. Isotype, *C.G. Pringle 13877* (US 462427).

FIG. 7. *Stenaria umbratilis* var. *brevipedicellata*. Holotype, *M.C. Johnston et al. 12032B*.

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